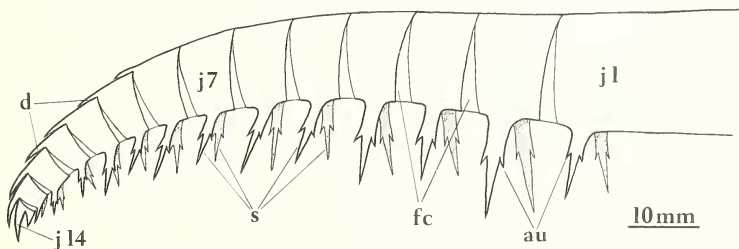


ANOMALOCARIS, THE LARGEST KNOWN CAMBRIAN ARTHROPOD

by D. E. G. BRIGGS

ABSTRACT. *Anomalocaris canadensis* Whiteaves, 1892, from the Middle Cambrian of British Columbia, is reinterpreted as an ambulatory arthropod appendage. Three further species from British Columbia, *A.?* *whiteavesi*, *A. gigantea*, and *A. cranbrookensis* are synonymized with the type. *A. pennsylvanica* from the Lower Cambrian of Pennsylvania is retained, but the affinities of some specimens remain equivocal and these are designated *A.?* cf. *pennsylvanica*. *A.?* *kokomoensis* and *A.?* *emmonsii* are removed from the genus. An additional appendage originally assigned to *Sidneyia inexpectans* Walcott, 1911a is redescribed and referred to as 'appendage F'; it may also belong to *Anomalocaris* and probably functioned in catching prey. The appendage-bearing arthropod is envisaged as multi-pedal with a dorso-ventrally flattened carapace extending laterally over the limb bases; it probably reached a length in excess of 1 m.

ANOMALOCARIS CANADENSIS was originally described by Whiteaves (1892) as a phyllocarid crustacean, the carapace of which was unknown. The genus has been interpreted as an arthropod trunk by subsequent workers, but no attempt has been made to explain why the anterior extremity has never been found attached (text-fig. 1). All species previously referred to the genus have been reinvestigated in an attempt to elucidate the morphology. *A.?* *kokomoensis* Ruedemann, 1925 and *A.?* *emmonsii* (Walcott, 1886) are removed from the genus, but their nature and affinities remain uncertain. *A. lineata* Resser and Howell, 1938, from the Lower Cambrian Kinzers Shale of Pennsylvania, represents the trunk of a trilobite-like arthropod, and has been removed to a new genus *Serracaris* Briggs, 1978b. The evidence suggests that the remaining species of *Anomalocaris* represent appendages of a large arthropod. Some of the large isolated limbs assigned by Walcott (1911a) to *Sidneyia inexpectans* have been shown by D. L. Bruton (in preparation) not to belong to this genus. They are similar in some respects to the appendage of *Anomalocaris*,



TEXT-FIG. 1. Reconstruction of ambulatory appendage of *Anomalocaris canadensis* Whiteaves, 1892, in lateral-oblique aspect.

and are likewise only known unattached. They are tentatively assigned to the genus *Anomalocaris* and referred to as 'appendage F'; they may belong to the same arthropod.

Terminology. The fossils are described as appendages; the basis for this interpretation is argued in the discussion. Directions on the appendages are given as dorsal, ventral and lateral, proximal and distal, assuming that they were attached to an unknown body at the incomplete end, the longest spines pointing ventrally. The slab upon which most of the thickness of a specimen remains on splitting is designated the *part*; the opposing slab, the *counterpart*. The following symbols are used on the text-figures: au, auxiliary spine; d, dorsal spine; fc, flexible cuticle or arthroal membrane separating segments; j1, j2 etc., segments numbered distally from that assumed to have been attached to the body; l, lateral spine; s, ventral spine (numbered where necessary to correspond with the segment bearing it). Breaks of slope are represented by hachures, the solid line at the upper edge of the break, the hachures directed downslope. The evidence upon which the reconstructions are based is illustrated, as far as possible, by the plates. The photographic technique was varied according to the nature of the preservation; this is indicated in the plate explanations. An interpretation of the specimens is presented where necessary as an adjacent camera lucida drawing.

Repositories. The following prefixes are used: BM—British Museum, Natural History; PA—North Museum, Franklin and Marshall College, Lancaster, Pennsylvania; GSC—Geological Survey of Canada, Ottawa; MCZ—Museum of Comparative Zoology, Harvard; MMK—Mineralogisk Museum, Copenhagen; ROM—Royal Ontario Museum, Toronto; SM—Sedgwick Museum, Cambridge; USNM—National Museum of Natural History, Washington, D.C.; YPM—Peabody Museum of Natural History, Yale.

Preservation. All the material of the appendages described is preserved compacted into the plane of bedding. *A. canadensis* and *A. pennsylvanica* are known preserved in one orientation only (Pls. 77–79), with the dorso-ventral plane lying in this plane (*lateral* aspect). All known specimens are curved ventrally towards the distal extremity; the evidence for the morphology of the joints suggests that the appendage would not completely straighten. This factor, in addition to the ventrally directed spines and flattened cross-section, presumably ensured that the appendage always came to rest lying on its side as it would have been unstable in any other attitude. Tilting of specimens relative to the bedding, however, accounts for slight variations in the configuration of the ventral spines. The individual spines of a pair may diverge due to tilting towards the proximal or distal end of the appendage (Pl. 77, fig. 5), or appear to differ in length as a result of tilting towards the dorsal or ventral margins (Pl. 78, fig. 3).

'Appendage F', in common with other arthropods occurring in the Burgess Shale, is preserved in a variety of orientations presumably due to a more circular cross-section, and the spines which project from each segment at high angles to each other (text-fig. 20). In *lateral* aspect the dorso-ventral plane lies in the plane of bedding (Pl. 81, fig. 2; Pl. 80, figs. 3, 4). The ventral spines are preserved at a high angle to the proximal segments of the appendage, and show little distal curvature. The auxiliary spines are orientated roughly normal to the bedding and are not much evident. More usually the ventral spines are rotated into the plane of bedding and show the pronounced distal curvature and the auxiliary spines borne on their anterior margin (Pl. 80, fig. 5; Pl. 81, fig. 4). The spines borne by the most distal segment are gently curved, and tend to be superimposed. Only the dorsal spines are preserved in outline against the matrix (Pl. 80, figs. 3, 4; Pl. 81, fig. 3). In *parallel* aspect the dorso-ventral plane is orientated normal to the bedding. The lateral spines are preserved in outline projecting from one side of the appendage (interpreted as anterior)—the ventral spines are superimposed on the other side, aligned parallel to the margin (Pl. 81, fig. 8; Pl. 80, figs. 1, 2, right appendage). The spines projecting from the terminal segment are directed to either side of the axis of the limb. The appendage usually occurs in an intermediate orientation. 85% of specimens are preserved in lateral or near lateral aspect; 12% approach parallel. Rare examples (3%) occur in near *vertical* aspect—the axis of the appendage approaching normal to the bedding and causing foreshortening, the ventral spines superimposed in outline (Pl. 81, fig. 1). The ventral spines commonly occur in isolation (Pl. 81, figs. 6, 7). In contrast to the walking appendage of *A. canadensis*, it is possible to identify the opposing individuals of a pair of 'appendages F' which are designated right and left assuming that the appendage projected laterally from the body and the lateral spines were borne on the anterior face (text-fig. 20). Where both appendages of a pair occur together they are usually preserved in different orientations to the bedding (Pl. 80, figs. 1, 2, 8).

SYSTEMATIC DESCRIPTIONS

Class, Order, and Family uncertain
Genus *ANOMALOCARIS* Whiteaves, 1892

Type species. Anomalocaris canadensis Whiteaves, 1892.

Other species. A. pennsylvanica Resser, 1929.

Occurrence. Lower Cambrian, Kinzers Formation, *Olenellus* Zone, Pennsylvania; Lower Cambrian, Eagar Formation, British Columbia; Middle Cambrian, Stephen Formation, *Bathyriscus-Elrathina* Zone, British Columbia.

Anomalocaris canadensis Whiteaves, 1892

Plates 77, 78; Plate 79, figs. 1–3; text-figs. 1–16

- v. 1892 *Anomalocaris canadensis* Whiteaves, pp. 205–208, fig. 1.
- v. 1902 *Anomalocaris canadensis*; Woodward, pp. 504, 505, 541–543, fig. 7.
- v. 1908a *Anomalocaris canadensis*; Walcott, pp. 244, 246, 247, pl. 2, fig. 3a, non fig. 3.
- v. 1908a *Anomalocaris* (?) *whiteavesi* Walcott, pp. 244, 246, pl. 2, figs. 4, 6, 6a, non figs. 2, 2a.
- v. 1912a *Anomalocaris canadensis*; Walcott, pp. 180, 197.
- v. 1912a *Anomalocaris gigantea* Walcott, pp. 153, 154, 156, 158, 159, 180, pl. 34, fig. 3.
- v. 1928 *Anomalocaris canadensis*; Henriksen, pp. 2, 13.
- v. 1928 *Anomalocaris gigantea*; Henriksen, pp. 13, 15.
- v. 1929 *Anomalocaris whiteavesi*; Resser, p. 12.
- v. 1929 *Anomalocaris cranbrookensis* Resser, pp. 6, 12, 15, pl. 2, fig. 4.
- v. 1969a *Anomalocaris canadensis*; Rolfe, p. 323, fig. 149, no. 2.
- v. 1975 *Anomalocaris gigantea*; Simonetta and Delle Cave, p. 7.
- v. 1975 *Anomalocaris* sp. Simonetta and Delle Cave, p. 7, pl. 5, fig. 13; pl. 50, figs. 2, 6.
- v. 1975 *Anomalocaris canadensis*; Simonetta and Delle Cave, pl. 5, fig. 8; pl. 50, figs. 1, 3–5.

Lectotype. GSC 3418 (designated herein), Plate 77, fig. 1, original of Whiteaves 1892, p. 206, fig. 1, *Ogygopsis* Shale, Mount Stephen.

Paralectotypes. GSC 3418a (Pl. 77, fig. 2), b, c, and d; GSC 359 (2 specimens) collected by McConnell (Whiteaves 1892, p. 207); GSC 355 (8 specimens and a slab with about 20), GSC 2020 (10 specimens and 2 slabs with about 12 and 5 specimens, respectively) collected by Ami (op. cit., p. 207); *Ogygopsis* Shale, Mount Stephen.

Other material. (*Ogygopsis* Shale, Mount Stephen, except where otherwise indicated.) BM 14763, original of Woodward 1902, p. 542, fig. 7; USNM 213687 (Pl. 77, fig. 3), original of Walcott 1908a, pl. 2, fig. 3a; USNM 213688, USNM 213689, and 213690 (Pl. 77, figs. 4, 5), syntypes of *A. whiteavesi* Walcott, 1908a, pl. 2, figs. 4, 6, 6a, respectively; USNM 57723 (Pl. 77, fig. 7), holotype of *A. gigantea* Walcott, 1912a, pl. 34, fig. 3, and counterpart, GSC 45307 (Pl. 77, fig. 6), Burgess Shale; MMK 1925.87 (Pl. 78, fig. 5), mentioned by Henriksen 1928, p. 13; USNM 80479 (Pl. 78, figs. 1, 2), holotype of *A. cranbrookensis* Resser, 1929, pl. 2, fig. 4, Cranbrook Shale, near Cranbrook; MCZ 5976, original of Rolfe 1969a, p. 324, fig. 149, no. 2, Burgess Shale.

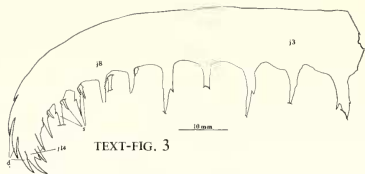
USNM 203136, 207253–207260, 213515–213543, 213559–213686, 213700–213735, 213884–213923, and additional fragments; USNM 189024–189026, 189164, 189166, 189167, 207248–207252, 213483–213514, and additional fragments, Burgess Shale; USNM 213694, Cranbrook Shale. GSC (numbers of individuals in brackets) 11526 (10), 11781 (16), 11953 (10), 12174 (1), 15409 (3), 35439 (7), and about 25 additional specimens; GSC 11496 (2), Burgess Shale; GSC 45308–45310, 45315–45319 and 6 additional specimens collected by the GSC expeditions of 1966 and 1967, Burgess Shale. MCZ 5974/1–5974/19, 3441 (3), and 10 additional specimens, all almost certainly *Ogygopsis* Shale, Mount Stephen (Rolfe (1962, p. 7) lists ‘ca. 22’ MCZ specimens from the Burgess Shale, but MCZ 5974/1–5974/19 are labelled ‘Raymond *et al.* Collection, 1930 and 1896’ (1896 prior to the discovery of Walcott’s Quarry) and the lithology appears to be that of the *Ogygopsis* Shale, Mount Stephen, rather than the Burgess Shale); MCZ 5974/20, 5974/21, Burgess Shale.

and all the known examples are preserved curved ventrally through up to 180° ; in extreme cases the terminal spines are directed towards the ventral margin of the proximal segments (Pl. 79, fig. 3). Each segment, apart from the 14th, bore a pair of elongate ventral spines at a point slightly proximal of the mid-length (Pl. 78, figs. 1, 3, 5). These spines alternated in length on successive segments; those borne on the even-numbered segments (apart from the 12th) were consistently longer than those on the odd. They were inclined to the ventral margin of the appendage (Pl. 78, fig. 3) at an angle decreasing from about 80° in the proximal segments to less than 50° in the most distal (these angles may be distorted during preservation). A pair of small ventrally directed, lateral 'auxiliary' spines diverged from a point just dorsal of the mid-length of each ventral spine at an angle of about 25° (Pl. 77, fig. 5; Pl. 78, fig. 3). The ventral spines tapered rapidly beyond this point. No evidence that they were segmented, or articulated at the base, has been observed. Rare variations in the morphology of the auxiliary spines include elongation and small spinose projections (Pl. 77, figs. 4, 5). The dorsal margin of segments 7 to 13 was produced distally into an elongate spine extending parallel to the appendage and overlapping the joints (Pl. 78, figs. 2-4). These spines became progressively larger and longer towards the distal extremity of the appendage. The 14th segment bore two terminal spines (Pl. 77, fig. 3; Pl. 78, fig. 3). The dorsal was elongate and curved, similar in outline to the dorsal spines of the segments immediately proximal to it; the ventral spine was blunt and triangular in outline, the margins straight or slightly concave. A series of small protuberances, elongate normal to the axis of the appendage, are preserved above the base of the paired ventral spines on some specimens (Pl. 77, fig. 6). These may represent points of attachment for intersegmental muscles.

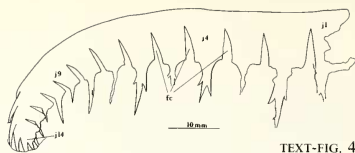
The proximal margin of each segment, apart from the first, was straight and inclined at about 80° to the dorsal margin of the appendage (Pl. 77, fig. 3; Pl. 78, fig. 4). A narrow triangular area, apex dorsal, of thinner cuticle along the distal margin of the segments presumably facilitated movement about the dorsally articulating hinge joints. The angle subtended by this area varies within a maximum of about 20° (Pl. 78, figs. 4, 6) and decreases in proportion to the curvature of the appendage (Pl. 79, fig. 3). The proximal margin of the triangle of flexible cuticle is generally not well defined; it appears to merge with the more heavily sclerotized region (Pl. 77, fig. 3; Pl. 78, fig. 4). No evidence for the presence of articulating structures at the hinge line has been observed; the segments appear to have been separated dorsally by a narrow band of thinner cuticle or 'arthrodial membrane' directed slightly proximally (Pl. 78, fig. 4). The joint between segments 13 and 14 is rarely well defined (Pl. 77, fig. 3) and may have been only partly functional.

The first segment was both longer and higher than the others and the evidence of a unique specimen suggests that it was attached proximally to the body (USNM 189024, Pl. 79, figs. 1-3). The appendage-body junction is obscured; a faint curved trace corresponds approximately in position and concave outline to the proximal extremity of complete examples (Pl. 78, figs. 1, 5) suggesting that the appendage usually fractured within the basal segment during or after moulting. There is no evidence of spines or gnathobase-like structures associated with the first segment but such features may be obscured by fragments of the body in USNM 189024. The ventral spines of this segment were borne closer to the joint with segment 2 than to the appendage-body junction. The unique 'body fragment' of USNM 189024 (Pl. 79, figs. 1-3) appears to be continuous with the appendage, and not part of some fortuitously superimposed structure. It consists of several layers of cuticle, similar to that of the limb, which appear to sandwich the first segment proximally. A small fan-shaped feature is superimposed on the proximal area of this segment and expands beyond the dorsal margin of the appendage into a gently convex distal margin. The proximal margin is semicircular, convex ventrally, the lateral margins concave. The distal area is made up of a series of closely spaced radiating lineations and appears to have been filamentous, consisting of several layers. The feature may represent a second ramus of the appendage but is omitted from the reconstruction (text-fig. 1) in the absence of further evidence. A semicircular feature ventral of the first segment of USNM 189024 bears a series of small, oblique marginal spines. This, together with the layers of cuticle surrounding the proximal extremity of the appendage, is interpreted as the crushed remains of part of the ventral cuticle of the body. A flattened, elongate parallel-sided structure aligned parallel and dorsal to the appendage (Pl. 79, fig. 3) lacks evidence of segmentation or spines. It may also represent part of the body, or an additional, poorly preserved appendage.

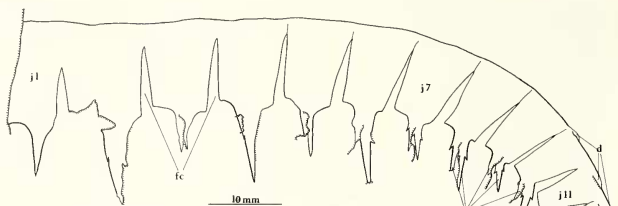
Morphometrics. The appendage is interpreted as one of a paired series but there is no apparent difference between the opposing lateral faces, and the right and left limbs cannot be distinguished. It has not proved possible to determine either the number of pairs borne by the arthropod nor the variation in morphology or size within or between individuals.



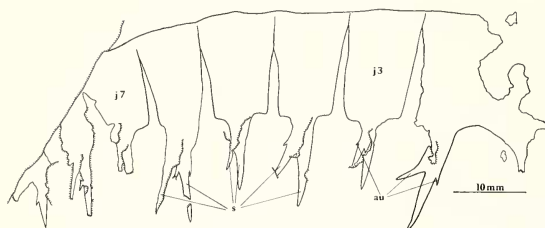
TEXT-FIG. 3



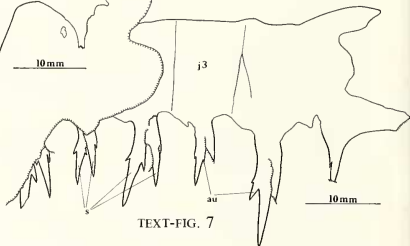
TEXT-FIG. 4



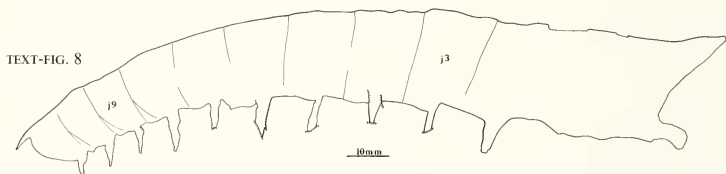
TEXT-FIG. 5



TEXT-FIG. 6



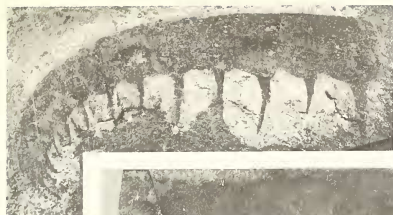
TEXT-FIG. 7



TEXT-FIG. 8

EXPLANATION OF PLATE 77

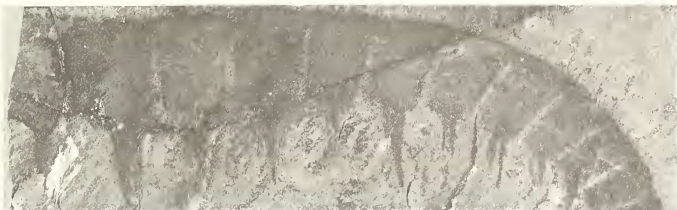
Figs. 1-7. *Anomalocaris canadensis* Whiteaves, 1892. 1, GSC 3418, lateral, north, ordinary light, $\times 1$, original of Whiteaves 1892, p. 206, fig. 1, background whitened by ?Whiteaves, *Ogygopsis* Shale, Mount Stephen; text-fig. 2. 2, GSC 3418a, lateral, north, ordinary light, $\times 1$, background whitened by ?Whiteaves, *Ogygopsis* Shale, Mount Stephen; text-fig. 3. 3, USNM 213687, lateral, non-directional, ordinary light, $\times 1.5$, original of Walcott 1908a, pl. 2, fig. 3a, *Ogygopsis* Shale, Mount Stephen; text-fig. 4. 4, USNM 213689, lateral, non-directional, ordinary light, $\times 1.5$, original of Walcott 1908a, pl. 2, fig. 6, *Ogygopsis* Shale, Mount Stephen; text-fig. 5. 5, USNM 213690, lateral, non-directional, ordinary light, $\times 1.5$, original of Walcott 1908a, pl. 2, fig. 6a, *Ogygopsis* Shale, Mount Stephen; text-fig. 6. 6, 7, GSC 45307 part, and USNM 57723 counterpart, lateral, uv light, $\times 0.8$, Burgess Shale; 6, part, west; 7, counterpart, south, reflected, original of Walcott 1912a, pl. 34, fig. 3; text-fig. 8.



1



2



3



4



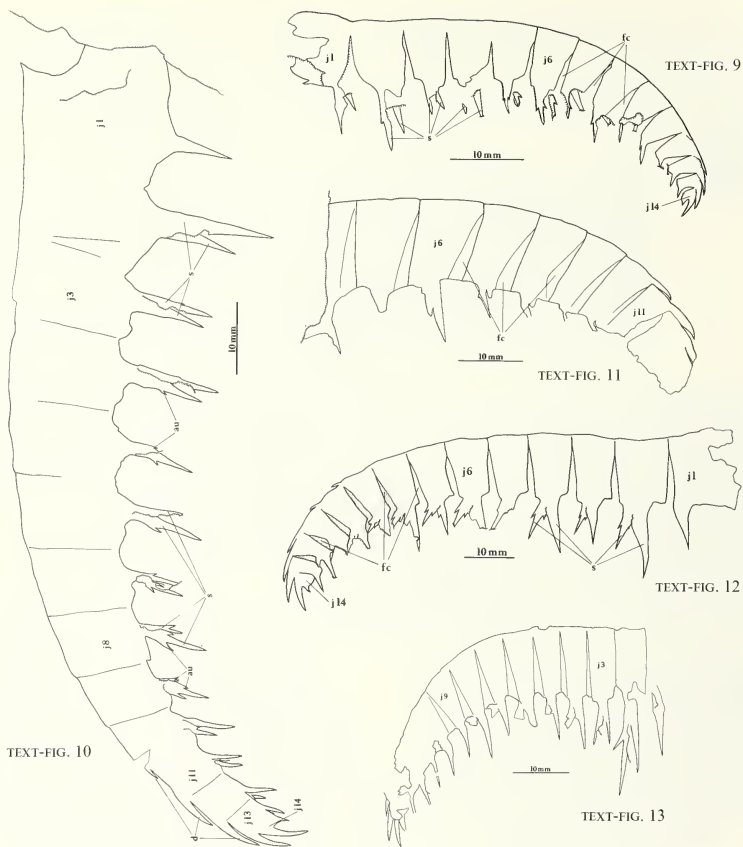
6



5



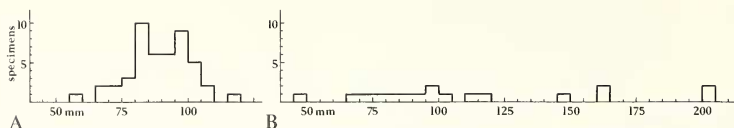
7



EXPLANATION OF PLATE 78

Figs. 1-7. *Anomalocaris canadensis* Whiteaves, 1892. 1, 2, USNM 80479, part and counterpart, lateral, non-directional, ordinary light, $\times 1.5$, Cranbrook Shale: 1, part, original of Resser 1929, pl. 2, fig. 4; 2, counterpart, showing distal spines; text-fig. 9. 3, GSC 45308, lateral, south, uv light, $\times 1.5$, Burgess Shale; text-fig. 10. 4, GSC 45309, lateral, north, ordinary light, under alcohol, $\times 1.5$, Burgess Shale; text-fig. 11. 5, MMK 1925.87, lateral, east, ordinary light, $\times 1$, *Ogygopsis* Shale, Mount Stephen; text-fig. 12. 6, SM A1448, lateral, north, ordinary light, $\times 1$, *Ogygopsis* Shale, Mount Stephen. 7, USNM 207259, lateral, north, uv light, $\times 1$, *Ogygopsis* Shale, Mount Stephen; text-fig. 13.

BRIGGS, *Anomalocaris*



TEXT-FIG. 14. Size-frequency histograms of appendage length of *Anomalocaris canadensis* Whiteaves, 1892, measured along the dorsal margin from the articulation between segments 1 and 2 to the distal extremity of the dorsal spine on segment 14. Data plotted in 5 mm intervals. A, *Ogygopsis* Shale, Mount Stephen, USNM locality 14s: mean 88.5, var. 149.7, N = 47. B, Burgess Shale: mean 113.4, var. 2098, N = 17.

Size frequency histograms for specimens from Mount Stephen and the Burgess Shale (text-fig. 14) are based on length measured along the dorsal margin of complete specimens from the joint separating the 1st and 2nd segments to the distal extremity of the dorsal spine borne by the 14th segment. The Mount Stephen material falls into a well-defined group between 55 and 120 mm long, with a mean of 88.5 mm. The Burgess Shale specimens show a much wider range from 45 to 205 mm, with a mean of 113.4 mm. The latter distribution may be bimodal but there is insufficient data to verify this (cf. *Canadaspis perfecta* (Briggs 1978a, fig. 177) and *Marrella splendens* (Whittington 1971, p. 1195) for example). The only known complete specimen from the Cranbrook Shale locality (Pl. 78, fig. 1) is 62 mm long, and thus falls within the size range at both the other localities.

Plots of the relative lengths of the segments (text-fig. 15) show an even decrease between segments 2 and 13, interrupted by segment 3 which was disproportionately short. The slight difference between samples from Mount Stephen and the Burgess Shale are considered to be a product of preservation and sample size.



TEXT-FIG. 15. Relative dorsal lengths of segments of *Anomalocaris canadensis* Whiteaves, 1892. Plot of dorsal lengths of segments of thirty-one specimens from the *Ogygopsis* Shale, Mount Stephen (solid line) and nineteen specimens from the Burgess Shale (dotted line) expressed as an average percentage of the total length of segments 4 to 10.

There is a strong correlation between the length of individual segments and the total length of several, suggesting that the relative lengths of the segments did not vary significantly with size. A lower degree of correlation exists between appendage length and that of individual ventral spines; the rare occurrence of specimens from Mount Stephen with unusually long spines (Pl. 78, fig. 7) provides further evidence of variability in their length.

Anomalocaris pennsylvanica Resser, 1929

Plate 79, figs. 4–6; text-figs. 17–19

- v. 1929 *Anomalocaris pennsylvanica* Resser, pp. 5, 6, 12, 17, pl. 5, fig. 5.
 v. 1938 *Anomalocaris pennsylvanica*; Resser and Howell, pp. 205, 231 *pars*, pl. 10, fig. 4 [cop. Resser 1929, pl. 5, fig. 5]; pl. 13, fig. 6, *non* fig. 5.

Holotype. USNM 80487, part (whereabouts unknown), original of Resser 1929, pl. 5, fig. 5, and counterpart, Plate 79, fig. 5 (USNM locality 12x).

Other material. YPM 14388 (Pl. 79, fig. 6), original of Resser and Howell 1938, pl. 13, fig. 6, Roger 1953, pl. 2, fig. 4, and counterpart, PA-387; YPM 10425 (USNM locality 12x). USNM 255611; PA-388, PA-389, PA-390 and ?PA-395a (USNM locality 22L).

Localities and stratigraphical horizon. Lower Cambrian, Kinzers Formation, *Olenellus* Zone: Getz Quarry, 1¼ miles north of Rohrertown, Pennsylvania (12x); ½ mile south of East Petersburg, Pennsylvania (22L).

DESCRIPTION

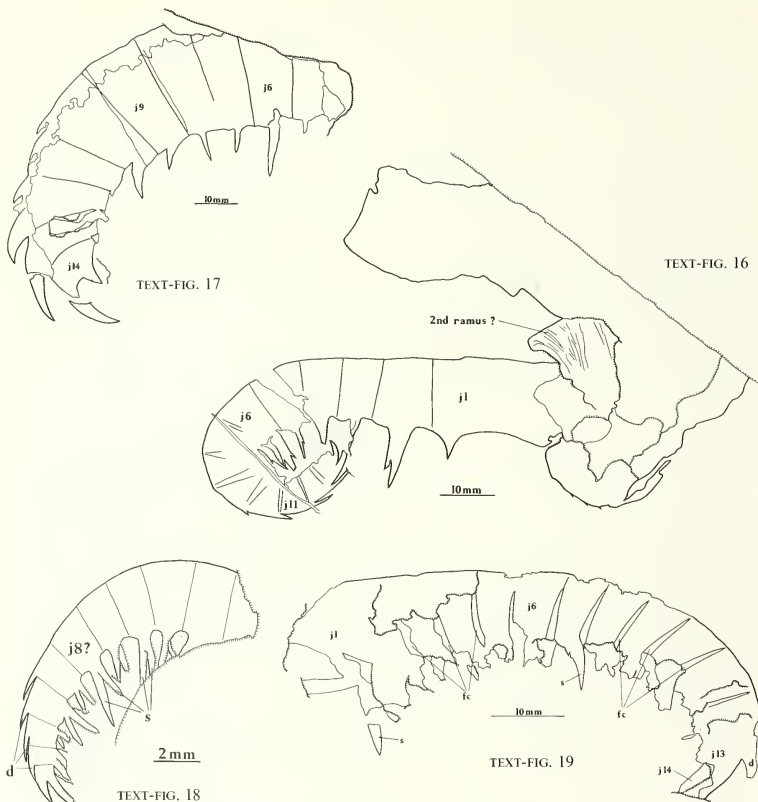
The relatively poor preservation and paucity of material from the Kinzers Formation makes a detailed description impossible, but the appendage was clearly similar to *A. canadensis*. It is only known preserved in lateral aspect, curved ventrally at the distal extremity. The whereabouts of the 'part' of USNM 80487 is unknown, but the indistinct published photographs (Resser 1929, pl. 5, fig. 5; Resser and Howell 1938, pl. 10, fig. 4) suggest that it consisted of fourteen segments; the counterpart (Pl. 79, fig. 5) is incomplete. Only one other known specimen (Pl. 79, fig. 6) includes the full complement of fourteen segments. Each segment bore a pair of ventrally directed spines which alternated in length on successive segments but were relatively longer, particularly in small examples (Pl. 79, fig. 5), than those of *A. canadensis*. The preservation is inadequate to show unequivocally that the longer spines were borne on the even-numbered segments as in *A. canadensis*, but this was likely the case. The apparent lack of auxiliary spines on the paired ventral spines is also probably a function of preservation. The joints appear to have articulated dorsally; the segments were separated by a triangular area of less sclerotized cuticle (Pl. 79, fig. 6). The distal segments bore dorsal spines overlapping these hinge joints.

The length of the holotype (along the dorsal margin from the joint between the 1st and 2nd segments to the distal extremity of the appendage) does not exceed 25 mm, based on the counterpart (Pl. 79, fig. 5) and Resser 1929, pl. 5, fig. 5. Most of the specimens are incomplete, but the length (estimated between the same points as on the holotype by extrapolation and comparison with *A. canadensis*) ranges from less than 30 mm (PA-388) to about 250 mm (PA-390, Pl. 79, fig. 4).

? Genus ANOMALOCARIS Whiteaves, 1892 'Appendage F'

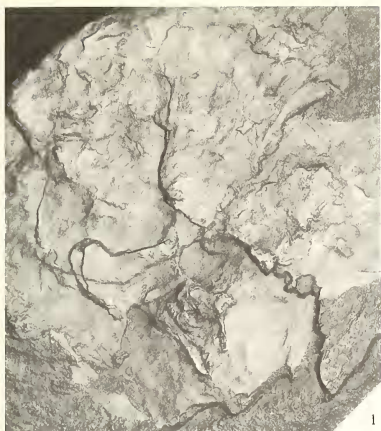
Plate 80; Plate 81, figs. 1–8; text-figs. 2, 20–32

- v. 1911a *Sidneyia inexpectans* Walcott *pars*, pp. 25, 26, pl. 4, figs. 1–4.
 1911b *Sidneyia inexpectans* Walcott *pars*, p. 517, figs. 1–4 [cop. 1911a, pl. 4, figs. 1–4].
 1916 *Sidneyia inexpectans* Walcott *pars*, p. 247, pl. 10, figs. 1–4 [cop. 1911a, pl. 4, figs. 1–4].
 1917 *Sidneyia inexpectans*; Burling, p. 78, fig. 2 *pars*.
 1928 *Sidneyia inexpectans*; Henriksen *pars*, pp. 18, 19.
 1944 *Sidneyia*; Størmer *pars*, fig. 17, no. 11, pp. 89, 124, 126, fig. 24b [figures after Walcott 1911a, pl. 4, fig. 4].



EXPLANATION OF PLATE 79

- Figs. 1-3. *Anomalocaris canadensis* Whiteaves, 1892; USNM 189024, part and counterpart, lateral, uv light, reflected, Burgess Shale: 1, part, east, $\times 2$; 2, counterpart, west, $\times 2$; 3, counterpart, north-west, $\times 1$; text-fig. 16.
- Figs. 4-6. *A. pennsylvanica* Resser, 1929. 4, PA-390, lateral, north-east, ordinary light, $\times 0.75$, Kinzers Formation, USNM locality 22L; text-fig. 17. 5, USNM 80487, lateral, south-east, ordinary light, $\times 4$, counterpart of original of Resser 1929, pl. 5, fig. 5, Kinzers Formation, USNM locality 12x; text-fig. 18. 6, YPM 14388, lateral, east, ordinary light, under water, $\times 1.5$, original of Resser and Howell 1938, pl. 13, fig. 6, Kinzers Formation, USNM locality 12x; text-fig. 19.



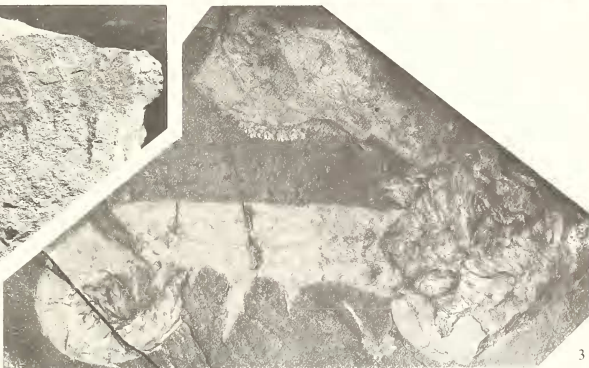
1



2



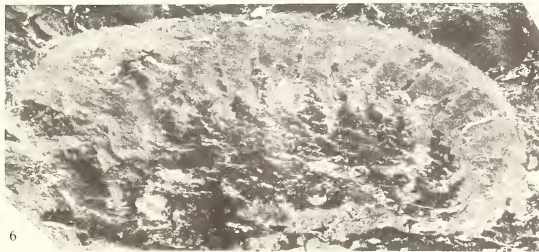
4



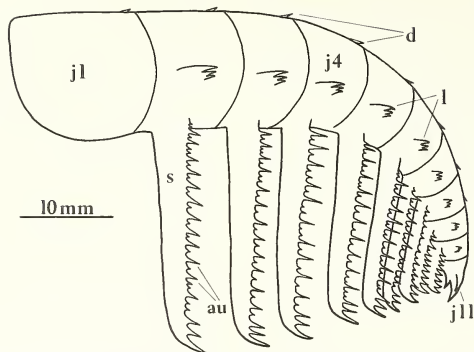
3



5



6



TEXT-FIG. 20. Reconstruction of a left 'appendage F' in anterior-oblique view.

- 1953 *Sidneyia*; Dechaseaux *pars*, p. 32, fig. 5.
 1959 *Sidneyia inexpectans*; Störmer *pars*, p. 26, fig. 16, no. 3, p. 30.
 v. 1963 *Sidneyia inexpectans*; Simonetta *pars*, pp. 99–102, figs. 1b, 2a, 2c, pl. 9 (non 139704); pl. 10 (non 139702, 139705, 139718); pl. 11 (non 139713, 139720).
 v. 1975 *Sidneyia inexpectans*; Simonetta and Delle Cave *pars*, p. 20, pl. 7; pl. 10, figs. 3, 4; pl. 11, fig. 5; pl. 12, figs. 6, 7; pl. 14, figs. 2–6; pl. 15, figs. 3–7 [pl. 10, figs. 3, 4; pl. 14, figs. 2, 6b *nov.*, otherwise cop. Simonetta 1963].
 1976 *Sidneyia inexpectans*; Simonetta *pars*, fig. 2 [cop. Simonetta 1963, figs. 1, 2].

Holotype. USNM 57490, part and counterpart (designated herein), Plate 80, figs. 1, 2, part original of Walcott 1911a, pl. 4, fig. 1.

Other material. USNM 57491–57493, originals of Walcott 1911a, pl. 4, figs. 2–4; USNM 139707, 139709–139711, 139717, 139719, 139721, 139724, 139726, originals of Simonetta 1963, pl. 9 and part of pl. 10. USNM 139706, 139675, 139684, 139687, 139690, 139691, 196285, 196294, 198832, 202227, 213866–213883, 240893–240991. GSC 10852, 45311–45314. MCZ 8894. Sixteen specimens in the collections made by the Royal Ontario Museum in 1975.

Locality and stratigraphical horizon. The appendage is known only from the Middle Cambrian Burgess Shale. The levels in the Walcott Quarry at which the four specimens collected by the GSC expeditions of 1966 and 1967 occurred are shown in text-fig. 2. All the USNM material bears the locality number 35k except for USNM 240952 (35k/1) and 240983 (35k/10) which may have come from the 'Raymond Quarry'. The associated fauna, which includes agnostids, *Marrella splendens*, *Isoxys acutangulus*, *Canadaspis perfecta*, and more rarely brachiopods, hyolithids, *Pagetia*, *Otoia prolifica*, *Scenella*, *Selkirkia*, *Mackenzia*, *Burgessia bella*, and *Sidneyia inexpectans* gives no indication of the levels from which the specimens were obtained.

DESCRIPTION

Specimens in which the maximum observed number of eleven segments are preserved (Pl. 81, figs. 2, 5) are considered 'complete' and are characterized by a comparable morphology regardless of size. In lateral aspect the appendage is always preserved curved ventrally (Pl. 80, figs. 3, 4; Pl. 81, fig. 2); it is probable

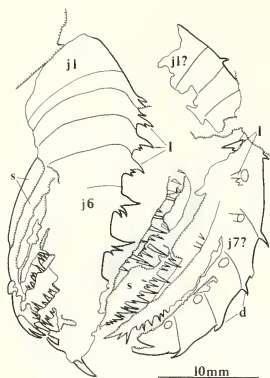
that, like the walking appendage of *Anomalocaris*, it could not be straightened. The degree of ventral flexure varies (Pl. 81, figs. 2, 5) although this is in some cases at least partly due to variations in orientation. Each segment, apart from the most proximal and distal, bore three spines, ventral, dorsal, and lateral (Pl. 81, fig. 3). A comparison of paired limbs preserved in different orientations (Pl. 80, figs. 1, 2) indicates that the appendage was subcircular in cross-section, flattened slightly dorso-ventrally and tapering distally.

A long ventral spine, bearing a series of auxiliary spines forming a comb-like structure, projected from the postero-ventral margin of each segment (except for the 1st and 11th). These ventral spines are characteristically preserved overlapping and compacted together (Pl. 80) and it is thus difficult to determine the precise distribution of the auxiliary spines. Slight variations in the proportions of isolated ventral spines (Pl. 81, figs. 6, 7) may simply reflect their variability within the series borne by the appendage (Pl. 81, fig. 4), or represent a change in successive instars with size increase. It is considered unlikely, however, that more than one pair of appendages of the arthropod is represented. There is no evidence of an articulation at the base of the ventral spines. Their attitude to the appendage does not appear to vary beyond the bounds accounted for by different orientations to the bedding. The ventral spines are directed at a high angle to the axis of the appendage in the proximal segments, and at a progressively lower angle toward the distal extremity (Pl. 80, figs. 3-7), thus ensuring that they remain in an approximately parallel configuration although the appendage is curved. The spines show no evidence of a tendency to disarticulate at the base; isolated examples are characteristically broken through the spine (Pl. 81, figs. 6, 7).

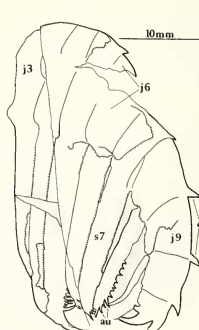
The ventral spines decreased in length towards the distal extremity of the appendage and show an increase in width through segments 8-10 (Pl. 80, fig. 5; Pl. 81, fig. 4). They were flattened in cross-section and presumably borne with this flattened plane normal to that of the appendage, the auxiliary spines pointing anteriorly. The ventral spines terminated distally in an auxiliary spine which curved parallel to the rest. The auxiliary spines decrease in number (from about thirty to about seven) as the ventral spines become shorter on the more distal segments of the appendage (Pl. 80, fig. 5). They are also apparently fewer in smaller specimens. The auxiliary spines vary in length along each ventral spine (Pl. 81, figs. 6, 7); a number of longer ones tend to be concentrated at the distal end. Those on the ventral spines borne by the more distal segments of the appendage tend to be longer throughout (Pl. 80, fig. 5; Pl. 81, fig. 4).

The dorsal margin of each segment, excluding the most distal and apparently the most proximal, was produced distally into a small dorsal spine, evident in lateral aspect, extending at an oblique angle to the limb (Pl. 80, figs. 3, 4; Pl. 81, fig. 3). Each segment also bore a more complex lateral spine, which may be preserved in outline in parallel aspect, projecting from what is assumed to have been the anterior margin of the appendage (Pl. 80, fig. 1; Pl. 81, fig. 8). The lateral spine included three separate spines projecting from a common base, decreasing in size and attached slightly more ventrally towards the distal margin of the segment. Apparent variations in this pattern within an appendage are probably largely the result of slight differences in the orientation of individual segments, due to the compression of the appendage into a plane normal to the curvature. The most distal (11th) segment bore three main spines; their preserved configuration varies considerably with orientation to the bedding. In lateral aspect the largest of the three is usually flanked by the remaining two, which decrease in size and are attached dorsal and ventral to it (Pl. 80, figs. 3, 4; Pl. 81, fig. 2). In parallel aspect the spines are splayed out on either side of the axis (Pl. 80, fig. 1), the largest usually between the other two (Pl. 81, fig. 8).

The articulations separating the segments are near normal to the dorsal margin of the appendage (Pl. 80, fig. 4; Pl. 81, fig. 1). Evidence for the configuration of flexible cuticle is poor, however, unlike that in the appendage of *A. canadensis*. The area of non-reflective film in USNM 57491 (Pl. 80, figs. 6, 7), for example, clearly does not correspond to the articulating membrane. The segments taper in outline ventrally in lateral aspect (Pl. 80, figs. 6, 7; Pl. 81, fig. 2), however, suggesting that the joints were hinged dorsally as in *A. canadensis* (cf. Pl. 77, fig. 3). The first segment was longer and larger than the rest, and bore no ventral spine (Pl. 81, figs. 2, 5); a lateral spine has not been observed and is assumed to have been also absent. The segment is subtrapezoidal in outline in parallel aspect (Pl. 80, figs. 1, 2) and appears to have tapered slightly towards the proximal extremity. In lateral aspect the dorsal margin is straight and well defined. The remainder of the free outline is convex and poorly defined; it presumably represents either the margin of the arthroal membrane at the appendage-body junction, or a line of weakness along which the first segment tended to fracture (cf. the appendage of *A. canadensis*). No trace of any projections or irregularities have been observed along this margin (Pl. 81, figs. 2, 5).



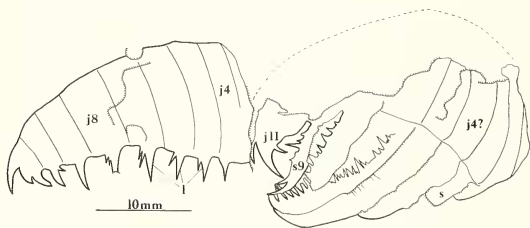
TEXT-FIG. 21



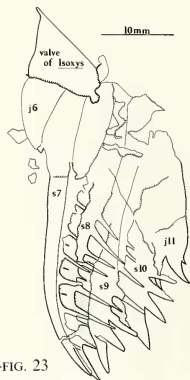
TEXT-FIG. 22



TEXT-FIG. 24



TEXT-FIG. 25



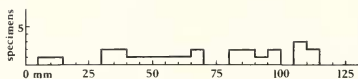
TEXT-FIG. 23

EXPLANATION OF PLATE 80

Figs. 1-8. 'Appendage F': Burgess Shale. 1, 2, USNM 57490, part and counterpart, pair of appendages—left lateral, right parallel, uv light, $\times 2$: 1, part, south, reflected, original of Walcott 1911a, pl. 4, fig. 1; 2, counterpart, east; text-fig. 21. 3, 4, USNM 57493, part and counterpart, right lateral, uv light, reflected, $\times 1.5$: 3, part, east; 4, counterpart, east, original of Walcott 1911a, pl. 4, fig. 4; text-fig. 22. 5, USNM 57492, left lateral, west, uv light, reflected, $\times 1.5$, original of Walcott 1911a, pl. 4, fig. 3; text-fig. 23. 6, 7, USNM 57491, part and counterpart, right lateral, uv light, reflected, $\times 2$: 6, counterpart, east, original of Walcott 1911a, pl. 4, fig. 2; 7, part, west; text-fig. 24. 8, USNM 139724, pair of appendages—left lateral, right parallel, south, uv light, reflected, under water covered by a glass slip, $\times 2$, counterpart original of Simonetta 1963, pl. 10; text-fig. 25.

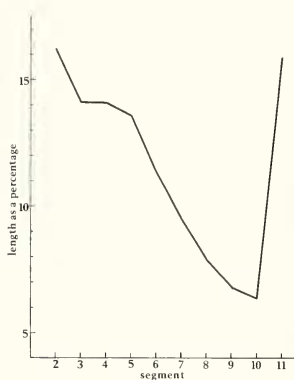


BRIGGS, *Anomalocaris*



TEXT-FIG. 26. Size-frequency histogram of length of 'appendage F' from the Burgess Shale measured along the dorsal margin from the articulation between segments 1 and 2 to the distal extremity of the dorsal spine on segment 11. Data plotted in 5 mm intervals. Mean 69.5, var. 1051, $N=25$.

The length of 'appendage F' (measured along the dorsal margin from the articulation between segments 1 and 2 to the distal extremity of the appendage) shows an even distribution ranging from 5 to 115 mm (text-fig. 26). USNM 196345 (Pl. 81, fig. 5) is the smallest known complete specimen. There is no evidence of a peak at any particular interval in the distribution but there are insufficient data to verify this. A plot of the relative lengths of individual segments (text-fig. 27) shows a similar configuration to that in the walking appendage of *A. canadensis*. Only the 3rd segment, which is relatively short, shows a pronounced departure from a gradual decrease in length between segments 2 and 10.



TEXT-FIG. 27. Relative dorsal lengths of segments of 'appendage F'. Plot of dorsal lengths of segments of sixteen specimens from the Burgess Shale expressed as an average percentage of the total length of segments 2 to 10.

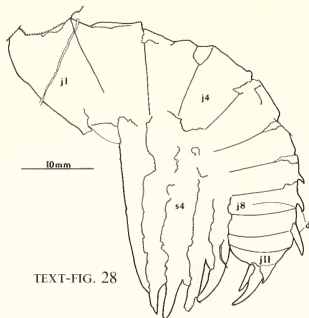
DISCUSSION

Previous interpretations of Anomalocaris canadensis. Three main variations of the hypothesis that *A. canadensis* represents an arthropod body have been put forward. Whiteaves (1892), and most later authors, considered that the ventral spines were the simple uropod or leaf-like appendages of a phyllocarid (Whiteaves 1892) or branchiopod (Walcott 1912*a*), the carapace of which was unknown. No evidence that the ventral spines were jointed, or that they articulated with the ventral margin of the segments has, however, been observed. They appear to have been continuous with

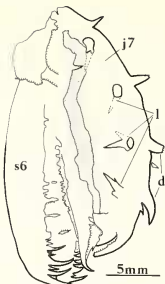
the rest of the cuticle and sclerotized to the same degree. Manton (1967, 1969) suggested that the ventral spines might represent a simple limb-lobe or lobopod such as that envisaged by Snodgrass (1958) as intermediate between the appendages of a lobopod worm and primitive arthropod. The objections to the first interpretation apply equally to this, and the pronounced alternation in length of the ventral spines on successive segments renders it even less likely that they could have served as the ambulatory appendages of a worm-like animal, or a myriapod as suggested by Jones in Whidborne (1896, p. 5). Simonetta and Delle Cave (1975, p. 7) discussed the possibility that *Anomalocaris* might represent the appendage of a large arthropod, but concluded that, although it could not be assigned with certainty to any bivalved carapace, it was more likely a body. They interpreted the ventral spines as 'spiniferous pleural lobes', basing their reconstructions (1975, pl. 5, figs. 8, 13) on a generalized interpretation of individual specimens.

Whiteaves (1892) interpreted the ventral spines of *A. canadensis* as 'probably branchial appendages', and considered the distal segments 'caudal' (1892, p. 205). His line drawing was based largely on the holotype (Pl. 77, fig. 1), which includes thirteen segments, although he recorded the number as ten or eleven (the text, and the legend to the figure, are contradictory in this respect). Woodward (1902, p. 542, fig. 7) figured a complete specimen adding a conjectural carapace and interpreted the areas of flexible cuticle separating the segments as a thin 'membranous connection which united the harder tergal portion of each somite to its fellow'.

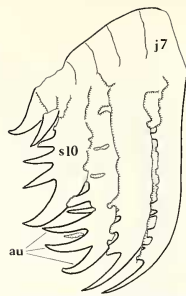
Walcott (1908a, pl. 2) figured two new species, *A. (?) whiteavesi* and *A. (?) acutangulus*, together with a specimen of *A. canadensis*, all from Mount Stephen, without descriptions or classification. *A. (?) acutangulus* is based on a valve of *Isoxys* Walcott, 1890. It is not clear on what basis Walcott separated *A. (?) whiteavesi* from *A. canadensis*. The intersegmental areas are less pronounced on his specimens of the former (compare Pl. 77, figs. 4, 5 with fig. 3) and are not included on the original figures (1908a, pl. 2, figs. 4, 6, 6a), but this difference is one of preservation. The three specimens figured as *A. (?) whiteavesi* (1908a, pl. 2, figs. 4, 6, 6a; two illustrated in Pl. 77, figs. 4, 5) are slightly larger than that of *A. canadensis* (1908a, pl. 2, fig. 3a; Pl. 77, fig. 3), and the spines correspondingly stouter. Walcott ascribed an isolated valve (1908a, p. 246, pl. 2, fig. 3), probably of *Canadaspis perfecta* (Briggs 1978a, p. 454) to *A. canadensis*, stating that it 'is the most abundant form of carapace'. He attributed fragments of a similar larger carapace (1908a, pl. 2, figs. 2, 2a), probably also *C. perfecta*, to *A. (?) whiteavesi*, which suggests that he considered this form to be rarer. There is no satisfactory evidence for retaining *A. (?) whiteavesi* as a separate species, and it is synonymized with *A. canadensis*. Walcott (1912a, p. 180, pl. 34, fig. 3) erected a further species, *A. gigantea* from the Burgess Shale, which he considered to differ from *A. canadensis* 'in its greater size and more compact abdominal segments'. The description was based on poorly preserved material, presumably all that had been collected by that time. The apparent 'compactness' is due to the loss of the tips of the ventral spines, which are not preserved on the 'part' of the holotype (1912a, pl. 34, fig. 3; Pl. 77, fig. 7), but are revealed by preparation of the counterpart (Pl. 77, fig. 6). Walcott considered that the ventral spines (which he interpreted as appendages) were 'composed of two joints' (1912a, p. 180) but no evidence has been observed to support this. The size range of *Anomalocaris* (text-fig. 14) from the Burgess Shale is



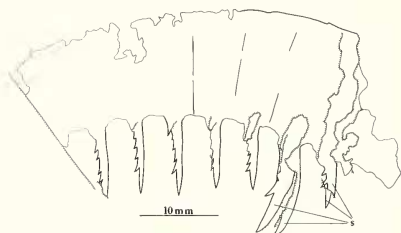
TEXT-FIG. 28



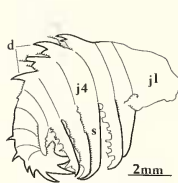
TEXT-FIG. 29



TEXT-FIG. 30



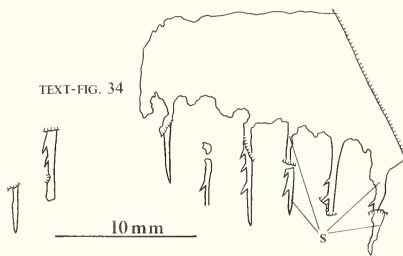
TEXT-FIG. 33



TEXT-FIG. 31



TEXT-FIG. 32



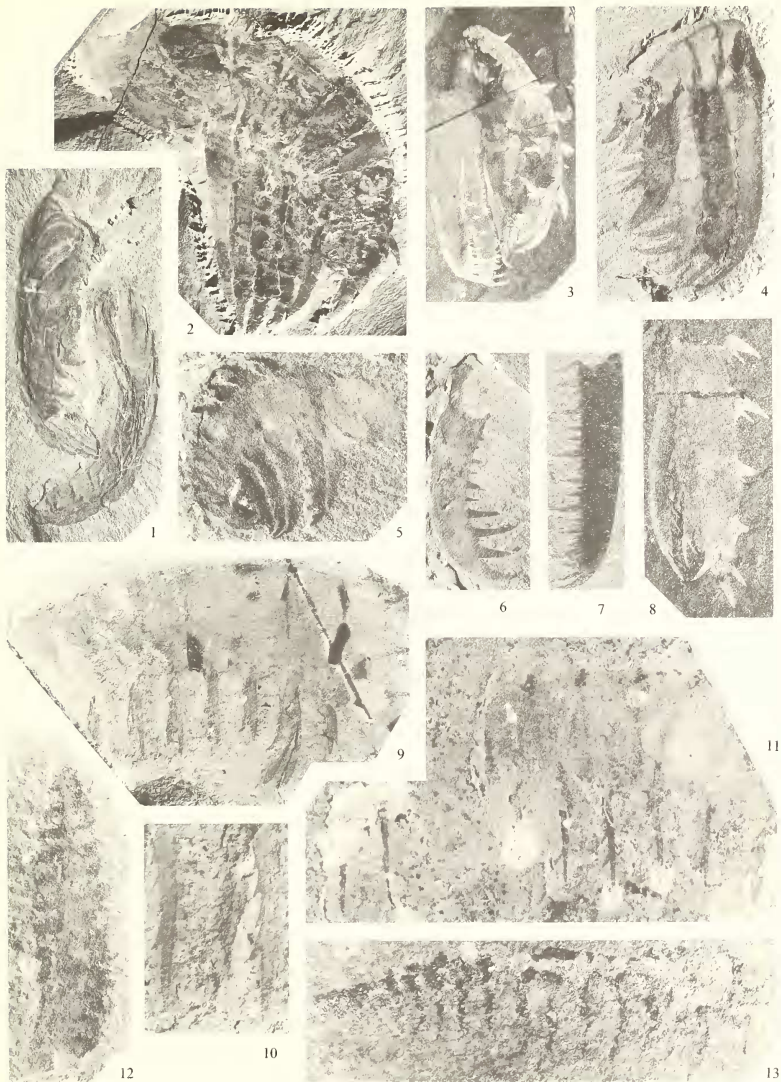
TEXT-FIG. 34



TEXT-FIG. 35

EXPLANATION OF PLATE 81

- Figs. 1-8. 'Appendage F': uv light, Burgess Shale. 1, USNM 240989, pair of appendages, vertical, east, $\times 1.5$. 2, USNM 240984, left lateral, north-west, $\times 1.5$; text-fig. 28. 3, USNM 139684, left lateral, west, reflected, under water covered by a glass slip, $\times 2$; text-fig. 29. 4, USNM 213880, left lateral, west, $\times 2$; text-fig. 30. 5, USNM 196345, left lateral, east, $\times 5$; text-fig. 31. 6, USNM 139709, isolated ventral spine, west, $\times 1.5$. 7, GSC 74987, isolated ventral spine, north, $\times 3$. 8, USNM 240987, left parallel, west, reflected, $\times 2.5$; text-fig. 32.
- Figs. 9-11. *Anomalocaris?* cf. *pennsylvanica* (Resser, 1929); ordinary light, Kinzers Formation, USNM locality 12x. 9, 10, USNM 213693, lateral: 9, north, $\times 1.5$; 10, north, $\times 4$, showing ventral spines; text-fig. 33. 11, USNM 90827, lateral, non-directional, $\times 3$; text-fig. 34.
- Figs. 12, 13. Indeterminate material previously referred to *Anomalocaris*. 12, *A.?* *emmonsii* (Walcott, 1886). USNM 92727, ordinary light, west, $\times 4$, original of Walcott 1886, pl. 11, fig. 5, Parker Quarry, Vermont. 13, *A.?* *kokomoensis* Ruedemann, 1925. NYSM 9627, ordinary light, south, $\times 1.5$, original of Ruedemann 1925, pl. 23, fig. 6, Kokomo Limestone, Indiana; text-fig. 35.



BRIGGS, *Anomalocaris*

much greater than on Mount Stephen, but in the absence of corresponding morphological differences the specimens are assumed to represent a single species. Walcott did not record *A. canadensis* from the Burgess Shale, so it is not known whether he considered all the specimens from the quarry to belong to *A. gigantea*. Rolfe (1962, 1963), however, referred some Burgess Shale specimens to *A. canadensis* when he curated the Raymond collection in the Museum of Comparative Zoology at Harvard.

Resser (1929) erected two new species, *A. pennsylvanica* and *A. cranbrookensis*. He recorded (p. 12) that the ventral spines of the former (which he interpreted as appendages) 'are relatively longer than in any of the described species'. *A. pennsylvanica*, like *A. canadensis*, was the appendage of a large arthropod, the body of which is unknown. The spines of small specimens (Pl. 79, fig. 5) are much longer than the vast majority of examples of *A. canadensis*; rare specimens of the latter, however, bore long spines (Pl. 78, fig. 7) and those of the largest known specimen of *A. pennsylvanica* (Pl. 79, fig. 4) are relatively short. *A. pennsylvanica* is poorly known compared to *A. canadensis*, and in the light of the apparent differences between them, is retained as a separate species. Resser and Howell (1938, p. 231) referred two additional specimens, YPM 14388 (Pl. 79, fig. 6) and USNM 90827 (Pl. 81, fig. 11), to *A. pennsylvanica*, but the latter is tentatively removed and described as *A.?* cf. *pennsylvanica* (p. 659). Resser (1929, p. 12) described *A. cranbrookensis* (Pl. 78, figs. 1, 2) as having 'about 14 or 15 abdominal segments and blunter appendages than *A. pennsylvanica*'. *A. pennsylvanica* is characterized (1929, p. 12) by having longer ventral spines than those of *A. canadensis*, hence the latter also bears the 'blunter appendages' of *A. cranbrookensis*. *A.?* *whiteavesi* is considered conspecific with *A. canadensis*, and Resser correctly observed the similarity of its 'caudal segment' to that of *A. cranbrookensis*. A re-study of the known material of *A. cranbrookensis* has revealed no justification for retaining it as a separate species. Simonetta and Delle Cave (1975, p. 7) erected a further species of *Anomalocaris* based on the presence of the auxiliary spines borne by the paired ventral spines. The apparent absence of these spines on other specimens, identified by Simonetta and Delle Cave as *A. gigantea*, is merely a function of preservation; the new species has no basis.

Henriksen (1928, p. 13) suggested, on the basis of a single specimen (Pl. 78, fig. 5) from Mount Stephen, that the 'body' of *Anomalocaris* could be divided into a thorax and abdomen. He interpreted segments 13 and 14 as one—'13 segments are present . . . of which the anterior 6 are small but distinctly broader and longer than the posterior 7'. The division is not pronounced, however, and is less significant with the interpretation of the specimen as an appendage. Henriksen suggested that *Anomalocaris* might have been the body of *Carnarvonina* or *Tuzoia*, an idea reiterated by Resser (1929). Rolfe (1969a, fig. 149, no. 2) figured an almost complete specimen of *A. canadensis* from the Burgess Shale and noted that the body consisted of 'at least 14 sub-quadrate segments' including the telson.

Reinterpretation. The preservation of *A. canadensis* provides several indications that it was not a body, but the appendage of a large arthropod. Resser (1929, p. 6) noted the association of the bivalved carapace *Tuzoia* with *Anomalocaris* in the Burgess Shale, Cranbrook Shale and the Lower Cambrian Kinzers Formation of Pennsyl-

vania, but this carapace is absent on Mount Stephen where *Anomalocaris* is most abundant. The layers of cuticle preserved proximal of the 1st segment of USNM 189024 (Pl. 79, figs. 1-3) do not appear to be part of a bivalved carapace, or cephalon, but may be interpreted as a fragment of compacted body cuticle. The small, fan-shaped, filamentous structure superimposed on the first segment of this specimen may represent an outer ramus. Disarticulated trunk somites of other Burgess Shale arthropods rarely occur, but appendages are relatively abundant. The preservation of other arthropods from the Walcott Quarry suggests that at least some specimens of *A. canadensis* from this locality would show traces of the alimentary canal or appendages if it were a trunk (and not exclusively represented by exuvia). The consistent lateral orientation is presumably mainly due to the curvature and projecting ventral spines, but suggests that the appendage was flattened antero-posteriorly in life. A trunk of this size would probably have been sufficiently wide to ensure the compression of at least some specimens dorso-ventrally, but no such examples have been identified. Two or three individual specimens from Mount Stephen are occasionally superimposed in parallel (Pl. 78, fig. 6), and examples of several preserved in approximately parallel attitudes on slabs are known. This might be the result of chance, or due to sedimentary processes, but some members of a series of appendages might equally be expected to retain their original relative positions during preservation where transport has been slight.

The morphology of *Anomalocaris* (text-fig. 1) lends additional support to its interpretation as an appendage. Hinge joints occur in the appendages of all arthropodan classes (Manton 1973). The trunk intersomite boundaries of most arthropods lacking a heavily mineralized exoskeleton, however, tend to consist of a band of flexible cuticle allowing movement in several directions. Similar paired spines occur on the appendages of several arthropod groups, including the eurypterids (Størmer 1974), arthropleurids (Rolfe 1969*b*) and in *Canadaspis perfecta* (Briggs 1978*a*). The ventral spines of *A. canadensis* are unlikely to represent pleural projections of a dorsal carapace. The number of segments is unusually large for an arthropod appendage, but thirteen or fourteen also occur in *C. perfecta*, and the euthycarcinoids (Gall and Grauvogel 1964; Schram 1971), for example.

Previous interpretations of 'appendage F'. Walcott (1911*a*) assigned the appendages described as 'appendage F' to *Sidneyia inexpectans*, although they are only known in isolation, and this interpretation has been accepted by all subsequent authors except D. L. Bruton (in preparation) who has convincingly demonstrated that they do not belong to this arthropod. Walcott (1911*a*, pl. 4, figs. 1-4) figured four examples of 'appendage F' which he interpreted as the 3rd appendage of *Sidneyia*. Burling (1917, fig. 2) transferred two of these (pl. 4, figs. 1, 4) directly on to an outline of *Sidneyia* achieving a totally implausible amalgam. Walcott's account of *Sidneyia* is further confused by his illustration (pl. 5, fig. 1) of a single appendage (USNM 57494) correctly referred to *Sidneyia* (Bruton, in preparation), but erroneously considered to represent three appendages, the 3rd, 4th, and 5th of the cephalo-thorax. This partly explains Walcott's (1911*a*, p. 25) assertion that the appendage varies considerably between large and small examples. In addition he did not fully understand the effect of variations in orientation to the bedding which explain the apparent

differences between the specimens illustrated in his pl. 4, figs. 1-4. Størmer (1944, p. 89; 1959) considered 'appendage F' to represent the first postoral appendage of *Sidneyia* (i.e. the 2nd rather than 3rd appendage in the sense of Walcott 1911a). He underestimated the number of segments as nine to ten.

Simonetta (1963, fig. 2c) reconstructed two paired appendages succeeding the antenna of *Sidneyia*, on the basis of material of 'appendage F'. These he assigned to the head, which he erroneously considered to include three tergal divisions, rather than a single cephalic shield (Bruton, in preparation). The identification of two different appendages rests on a misinterpretation of a few specimens which are unusually orientated with respect to the bedding (1963, p. 101). Simonetta considered USNM 139724 (1963, pl. 10; Pl. 80, fig. 8) to represent both of these appendages in association. This specimen consists, however, like the holotype (Pl. 80, figs. 1, 2), of a pair of appendages, the left and right preserved in different orientations to the bedding. The right appendage of USNM 139724 (Pl. 80, fig. 8), the basis for Simonetta's first 'raptorial' appendage, is compacted in parallel aspect. The lateral spines are preserved in outline directed anteriorly, the ventral spines lie within the matrix beneath the exposed dorsal surface. The left appendage (Simonetta's second) is preserved in near lateral aspect, each ventral spine overlapping that borne by the segment proximal to it. The surface of the appendage exposed is essentially the posterior; the ventral spines are rotated into the plane of bedding, but it is clear that the auxiliary spines are directed at an oblique angle 'into' the slab (i.e. anteriorly). Simonetta's (1963, p. 101) description of his 'second' appendage corresponds in general outline to the more detailed account of 'appendage F' presented above; while he underestimated the number of segments as eight, he observed both lateral and ventral spines. Simonetta recognized that the comb-like ventral spines occurred in isolation but exaggerated their variability; his eight types (1963, p. 101, pl. 9) are mainly based on fragments, and at least partly preservational. He states, in addition, that the auxiliary spines are equal throughout the appendage USNM 57492 (1963, p. 101), whereas more detailed examination of the specimen (Pl. 80, fig. 5) shows that this is not the case. It is not clear how Simonetta (1963, p. 102) arrived at a thickness of 2 mm for the cuticle in the isolated segment represented by USNM 139707 (pl. 9); this figure includes a considerable proportion of matrix. Simonetta (*in* Simonetta and Delle Cave 1975) reiterated his opinion that 'appendage F' belonged to *Sidneyia*. The example *in situ* which he cited as figured by Walcott (1911a) and Størmer (1944) refers to USNM 57487; the appendage in question is a trunk of *Waptia* protruding from beneath the carapace.

Functional morphology. The multisegmented appendage of *A. canadensis* (text-fig. 1) was presumably ambulatory in function, although a large flattened limb would also have facilitated swimming. Manton (1973) pointed out that simple articulations between segments of similar diameter restrict the flexibility of an appendage and suggested that a large number of segments might be expected to compensate for this. *Anomalocaris* may reflect this condition; the articulations appear to have been similar in the terrestrial Carboniferous *Arthropleura armata* (Briggs, Rolfe, and Brannan 1979), which Manton cited as an example. The segments are undifferentiated throughout the length of the appendage of *A. canadensis*, and do not appear to have

overlapped to a great degree. Movement about the articulations was presumably achieved by a pair of flexor muscles extending from the dorsal margin of each segment to the small protuberance at the base of the ventral spines in the segment distal to it (Pl. 77, fig. 6). The thinner cuticle separating the segments permitted a downward flexure—the amplitude of movement was limited by the width of flexible cuticle and degree of overlap but appears to have been sufficient to allow a curvature of the appendage through 180° (Pl. 79, fig. 3). The extension of the limb could thus have been varied during walking. The relatively short 3rd segment (text-fig. 15) presumably increased the ventral flexure at this point. The force exerted on the distal articulations of the appendage in contact with the substrate would have been considerable due to the length of the limb, and the weight of the large body. The dorsal spines overlapping the articulations may have helped to prevent them fracturing under this force. The articulation separating segments 13 and 14 is not well defined and may have resembled that across the tarsus in lysiopetaloid myriapods, in which the cuticle is undivided dorsally but slightly thickened and probably elastic, so forming an incipient hinge (Manton 1958, p. 524).

The 'terminal claw' and spines on the distal segments in *Anomalocaris* may have prevented the limb from slipping or shifting on the substrate (cf. Manton 1952, with reference to the Myriapoda). The paired ventral spines of several of the more distal segments may have come into contact with the substrate when the appendage was fully extended, thus achieving a strong foothold, or preventing the leg from sinking into soft sediment. Størmø (1974, p. 363) has suggested this function for the distal spines of a similar appendage (with fewer segments) in the eurypterids, which was primarily used for walking. The ventral spines on the more proximal segments would not, however, have made contact with the substrate during the normal gait of either an eurypterid (Hanken and Størmø 1975) or presumably *Anomalocaris*. The apparent flexibility of the *Anomalocaris* appendage suggests that opposed individuals of a pair, or even individual limbs, could have been used for grasping prey (cf. Whittington 1975, *Olenoides serratus*). The ventral spines might also have facilitated digging and raking the sediment in pursuit of prey.

The function of 'appendage F' has been briefly discussed by previous authors who assumed that it belonged to *Sidneyia*. The appendage was not 'chelate' as stated by Walcott (1911a, p. 26), who considered that it may have functioned in 'capturing the numerous small phyllopod crustaceans and numerous annelids with which the bottom and adjacent water were abundantly supplied'. He further suggested the possibility that the appendages 'were also used in fighting and that there was a marked difference in those belonging to the male and female'. No evidence of a difference in morphology between specimens of 'appendage F' has been noted which could be ascribed to sexual dimorphism. The appendage seems ill-adapted for 'fighting' and equally for walking in which it would have been hindered by the long ventral spines with their array of auxiliary spines. It might have facilitated swimming but is most likely to have functioned in food capture.

Størmø (1944) argued that both appendages of the pair might together have served as a catching apparatus similar to that in the eurypterid *Mixopterus* (cf. Hanken and Størmø 1975), an idea reiterated by Dechaseaux (1953). It seems unlikely that 'appendage F' served to break up food, in addition to trapping it, as suggested by

Simonetta (1963, pp. 104, 105); this function was presumably performed by additional unknown structures or appendages.

It may be assumed that, in view of the specialized nature and postulated feeding function of the appendage, it was borne at the anterior end of the arthropod, probably by the cephalon. The joints apparently allowed limited movement laterally as well as flexure ventrally. 'Appendage F', like the walking appendage of *Anomalocaris*, does not appear to have straightened dorsally, and the ventral spines were apparently graduated in length so that the distal extremities formed an approximately straight line, the ventral spines parallel, when the appendage was flexed ventrally in its usual preserved attitude. The degree of movement possible at the appendage-body junction is unknown, but both appendages of a pair might have been extended laterally to sweep the substrate as the arthropod progressed, and brought together medially to trap prey. The anteriorly directed auxiliary spines would have been particularly suitable for ensnaring and impaling soft-bodied forms: transfer to the mouth must have been achieved by an additional unknown appendage. Such unknown structures must also be involved if, as Rudkin (in press) suggested, *Anomalocaris* was responsible for wounds inflicted on the trilobite *Ogygopsis klotzi*.

The lack of a body. The most intriguing aspect of the preservation of both *Anomalocaris* and 'appendage F' is the lack of other identified body-fragments. The largest arthropods found in association with these appendages occur in the Burgess Shale and are *Sidneyia* Walcott, 1911a (Bruton, in preparation), *Helmetia* Walcott, 1918, and *Tegopelte* Simonetta and Delle Cave, 1975, which reach lengths of about 170 mm, 180 mm, and 300 mm respectively, but the appendages of these genera are known, and are unlike those in question. The largest isolated carapaces are those of the bivalved arthropods *Tuzoia* and *Carnarvonina*, up to 120 mm and 88 mm in length respectively. The smallest specimens of *Anomalocaris* from British Columbia, however, are almost half the length of the former, and although much smaller examples of 'appendage F' are known, the considerations outlined below suggest that the appendages are unlikely to have belonged to bivalved forms. The predominance of incomplete appendages suggests that the specimens represent exuvia, or fragments of dead individuals. Only 37% (sample size 59) of the specimens of *A. canadensis* from the Burgess Shale held by the National Museum in Washington are complete, but this figure is probably exaggerated by collecting bias; the figure for the Geological Survey of Canada collections of 1966 and 1967 (Whittington 1971) is only 6% (sample 19). The degree of completeness at the Mount Stephen locality is apparently higher; 23% exclusive of large slabs (sample 202), 20% on large slabs alone (sample 55). The National Museum specimens of 'appendage F', which only occurs in the Burgess Shale, reveals 28% complete (sample 99) excluding fragments of spines, but only 20% (sample 140) if these are included assuming that each represents a single appendage. The complete state of most of the Burgess Shale fossils suggests that they were not carried far, but buried by turbidity-current-transported sediment almost *in situ*. There is little evidence of transport off the reef top, but incomplete animals represented by the appendages described herein, and by isolated carapaces like *Tuzoia*, might have originated at intermediate depths and been carried further than the other elements of the fauna.

Several factors may be invoked to explain the lack of evidence of body fragments, but all imply separation of the appendages from the body during transport. The cuticle of the appendages may have been more heavily mineralized, and thus more resistant to disintegration than that of the body (as are the claws of Recent Brachyura, for example). The exoskeleton of most Recent crustaceans is altered by resorption of calcareous material prior to moulting, making certain regions brittle 'mainly at the bases of the limbs and claws' (Schäfer 1972, p. 434). Similar changes may have occurred in this case, facilitating the separation of the limbs from the body. The appendages are less likely to represent remains of carcasses, which in contrast with exuvia, tend to retain the appendages attached (cf. Schäfer 1972, p. 138). The body of a large arthropod might, however, float due to gas released by the processes of decay, and shed the limbs before sinking itself. Even in the unlikely event of the body being sclerotized to a much lesser degree than the appendages, if it were present, some trace would almost certainly have been preserved. The large accumulations of up to fifty appendages of *A. canadensis* on a single slab from Mount Stephen may represent the simultaneous release of the exuvia of several individuals of a single generation (cf. Schäfer 1972, p. 437) and suggests that this occurrence must be closest to the habitat of the arthropod. Large, previously unidentified, relatively featureless fragments of the body cuticle of *A. canadensis* almost certainly await discovery on the scree slopes of Mount Stephen. The isolated examples of *A. canadensis* and 'appendage F' which occur in the Phyllopod bed show a much wider size range and are probably fragments of exuvia which were occasionally carried in. Schäfer (1972, p. 431) noted, for example, that the carapace and abdomen of the Recent natantian decapods 'have a tender skin and contain little calcareous material; thus even slight transportation destroys these parts of the exuvia. What remains are the most heavily calcified rostral areas and especially the hard claws'. The appendages of eurypterids and other fossil arthropods (e.g. *Cyrtoctenus* Stormer and Waterston, 1968) are often preserved in isolation. Some differences between the Burgess Shale fauna and that of the stratigraphically older fossil beds on Mount Stephen have yet to be explained. Both trilobites and *A. canadensis* are very much more abundant on Mount Stephen, for example, but the latter shows a much more restricted size distribution than in the Burgess Shale. The contrasts are presumably a combination of age, palaeoecology, preservation, and the nature and distance of transport, although both deposits are similar in origin and position relative to the reef front (McIlreath 1974).

Affinities and classification. It is tentatively suggested that 'appendage F' and the walking appendage of *A. canadensis* belonged to the same, or at least similar, arthropods, although the lack of the former on Mount Stephen, for example, where *A. canadensis* is so abundant, cannot be explained. Data on the precise levels in the Burgess Shale quarry at which the limbs were found (text-fig. 2) indicate that examples of both occur at some horizons. The appendages are known only in isolation and are some of the largest fossils in the Burgess Shale, both achieving a comparable size (text-figs. 14, 26). The two appendages are similar in gross morphology, and are characterized by an unusually large number of segments. They further complement each other functionally. The over-all uniformity and simple structure of the walking appendage of *A. canadensis*, together with its abundance in individual beds on Mount

Stephen, suggest that the trunk may have borne many pairs. (Some eurypterids, however, walked on three pairs of limbs (cf. Hanken and Størmer 1975, p. 265), the anterior two not greatly dissimilar to these.) A single pair of 'appendages F' may be envisaged on the cephalon, in addition to other unknown limbs, which were employed in feeding.

A possible relationship between the limbs, however, remains equivocal. A number of features of their preservation and distribution appear to invalidate the hypothesis, but these may be at least partly enigmatic characteristics of the deposits in which they occur, and not peculiar to the taphonomy of the appendages alone. About 40% of the specimens of *A. canadensis* in the Walcott collection, and in that made by the GSC expeditions, came from the Raymond Quarry. On the other hand the GSC collected no specimens of 'appendage F' from the Raymond Quarry, and material from that horizon constitutes only about 1% of the National Museum collection. If 'appendage F' is indeed a specialized cephalic appendage, as the interpretation above suggests, it should be much rarer than the walking appendage. This is borne out by the GSC collection (ratio 4:18) but not by the Walcott collection in which 'appendage F' is about twice as common as *A. canadensis*. 'Appendage F' also occurs in much smaller sizes (text-figs. 14, 26). These factors may perhaps be explained by the vagaries of preservation; Walcott may have found a pocket rich in 'appendage F'. More peculiar features of the Burgess Shale include, for example, the preservation of appendages in so few of the trilobites. More striking is the absence of 'appendage F' from other localities where *A. canadensis* occurs, particularly, on Mount Stephen where the latter is extraordinarily abundant. An appendage somewhat similar in morphology (*A.?* cf. *pennsylvanica*) does, however, occur in the Kinzers formation in association with *A. pennsylvanica*.

Whether or not they belong to the same or similar arthropods the morphology of the appendages gives little indication of affinity. Similar simple joints occur in the limbs of all arthropodan classes (cf. Manton 1973). Limbs with a large number of segments are rare, but occur in groups as diverse as the arthropleurids (Rolfe 1969*b*), phyllocarids (Briggs 1978*a*), and euthycarcinoids (Gall and Grauvogel 1964; Schram 1971). Paired ventral spines also occur in all these groups, and in the eurypterids (Størmer 1974). The walking appendage of *A. canadensis*, however, may have been biramous, and this would eliminate it from the essentially terrestrial Myriapoda and Arthropleurida. It is unlikely to have given rise directly to a limb of fewer segments, by fusion of those bearing alternately longer and shorter paired spines, for example. The arrangement of the articulations and ventral curvature suggests that both limbs projected laterally from the body, the ventral spines directed downwards, and the distal extremity in contact with the substrate. The carapace was therefore probably flattened dorso-ventrally, extending over the basal limb segments, rather than bivalved, as in the phyllocarids. The arthropod bearing these appendages might belong to almost any class, even representing an early marine myriapod-like group.

Comb-like structures referred to the Angustidontidae Cooper, 1936 (see Copeland and Bolton 1960 for a review) which are very similar to some examples of the ventral spines of 'appendage F' occur isolated in rocks from Silurian to Lower Mississippian age in North America. Unlike the ventral spines of 'appendage F', however, *Angustidontus* was apparently attached at the proximal end by a 'ball and socket' type of

articulation (Copeland and Bolton 1960, p. 36; confirmed by J. Berdan, pers. comm., on the basis of a specimen from locality USGS 4982-SD, Upper Devonian, Carlin quadrangle, Nevada). Dr. Berdan considers that the *Angustidontidae* are arthropod rather than vertebrate remains. Their affinities may lie with the eurypterids, and they are unlikely to represent the arthropod bearing 'appendage F', although they may have been similar in function to the ventral spines of the latter.

Manton (1954) considered that the size of arthropods was limited by such factors as difficulty incurred in moulting and, in the case of millipedes, by the leverage which could be exerted by the appendages. The weight was presumably buoyed up in a marine environment, reducing the strain on the limbs. The largest appendages of *Anomalocaris canadensis* are over 200 mm in length (USNM 213483, 213484 from the Burgess Shale) and extrapolation suggests that the largest example of *A. pennsylvanica* (Pl. 79, fig. 4) may have reached 250 mm. 'Appendage F' exceeds 115 mm. The sizes which some arthropods would assume if their appendages were of this dimension are as follows: *Arthropleura armata* (Rolfe 1969b), 3.0 m; *Carcinosoma scorpionis* (Clarke and Ruedemann 1912), 1.1 m; *Euthycarcinus kessleri* (Gall and Grauvogel 1964), 2.0 m. It seems reasonable to suggest that the arthropods bearing the isolated appendages may have reached lengths of at least 1 m, a size in excess of any previously recorded Cambrian arthropod. Isolated segments and paratergal folds of the Carboniferous *Arthropleura* have been found which indicate that it attained lengths of up to 1.8 m (Rolfe 1969b) which is about the size reached by the eurypterid *Pterygotus*, the largest arthropod known (Størmer 1955).

Anomalocaris? cf. *pennsylvanica* (Resser, 1929)

Plate 81, figs. 9-11; text-figs. 33, 34

v. 1938 *Anomalocaris pennsylvanica?*; Resser and Howell, p. 231 pars. ?pl. 13, fig. 5; non pl. 10, fig. 4; pl. 13, fig. 6.

Material. USNM 213693 (Pl. 81, figs. 9, 10) and counterpart, PA-394; USNM 90827 (Pl. 81, fig. 11) and counterpart, PA-393. Resser and Howell figured a specimen (1938, pl. 13, fig. 5) described in the legend (p. 231) as USNM 90827; it is not clear from their photograph which, if either, of the above specimens, both originally numbered USNM 90827, was illustrated.

Locality and stratigraphical horizon. Lower Cambrian, Kinzers Formation, *Olenellus* Zone, $\frac{1}{2}$ mile south of East Petersburg, Pennsylvania (USNM locality 22L).

DESCRIPTION

The two incomplete specimens known are interpreted as arthropod appendages and appear to have been compacted in lateral aspect (cf. *A. canadensis*). At least seven segments are evident in USNM 213693 (Pl. 81, fig. 9) and nine in USNM 90827 (Pl. 81, fig. 11). The intersegmental boundaries are approximately normal to the dorsal margin of the appendage; a series of dark spots along the dorsal margin of USNM 90827 (Pl. 81, fig. 11) may represent the position of the articulations, indicating that the joints were hinged. The appendage tapered gradually (presumably distally) and each segment bore a pair of elongate ventral spines. A series of at least four small, ventrally directed, equally spaced auxiliary spines (Pl. 81, figs. 9-11) are preserved projecting from the margin facing the direction in which the appendage tapered. One segment of USNM 213693 (Pl. 81, fig. 9) bore longer, stouter ventral spines which curved distally. There is no unequivocal evidence that the ventral spines were segmented. Those of USNM 90827 (Pl. 81, fig. 11) appear to have been almost equal in length to the height of the segments, whereas in USNM 213693 (except for

the larger pair) they only approach this length in the more 'distal' of the preserved segments (Pl. 81, fig. 9). USNM 90827 may represent the more distal shorter segments of the same appendage as the other. The length along the dorsal margin of the six relatively complete segments of USNM 213693 is about 40 mm. The distance between the spines preserved at opposite ends of USNM 90827 (i.e. equivalent to the approximate length of eight segments) is 25 mm.

DISCUSSION

Resser and Howell (1938, p. 231) apparently referred one of these specimens to *A. pennsylvanica* and hence interpreted it as the body of a crustacean. The straight ventral spines, however, do not appear to have articulated proximally, and the lack of variation in their preserved attitude to the 'body' suggests that they do not represent appendages. The elongate outline of the spines makes it equally unlikely that they were the lateral extensions of tergites. The specimens are tentatively referred to *A. cf. pennsylvanica*, although the ventral spines apparently differed, in the absence of more completely preserved material to prove otherwise. The possibility that they represent a different appendage of the same arthropod (the same relationship as that postulated between *A. canadensis* and 'appendage F') cannot be entirely ruled out.

INDETERMINATE MATERIAL PREVIOUSLY REFERRED TO *ANOMALOCARIS*

Anomalocaris? *kokomoensis* Ruedemann, 1925

Plate 81, fig. 13; text-fig. 35

v. 1925 *Anomalocaris* (?) *kokomoensis* Ruedemann, pp. 75, 76, pl. 23, fig. 6.

Holotype. NYSM 9627, Plate 81, fig. 13, original of Ruedemann 1925, pl. 23, fig. 6.

Other material. Unknown.

Locality and stratigraphical horizon. Upper Silurian, Late Ludlow-Pridoli, Salina Formation, Kokomo Limestone Member, Kokomo, Indiana.

DESCRIPTION

The specimen (Pl. 81, fig. 13) is preserved as a discontinuous thin layer of dark material in a fine-grained, laminated limestone. It is elongate (55 mm in length), tapering in one direction, and bears a series of thirteen projections approximately normal to the longitudinal axis, which curve distally towards the tapered extremity.

DISCUSSION

The specimen is rejected from *Anomalocaris* to which Ruedemann (1925, p. 75) tentatively assigned it, interpreting it as a body with 'about 17' appendage-bearing segments. It is too poorly preserved to permit a satisfactory description or identification. The projections or 'ventral spines', in contrast to those of *Anomalocaris*, curve distally, and there is no evidence that they were paired, or alternated in length on successive segments. They do not show the same spatial arrangement as the spines of *Anomalocaris*, which were regularly spaced; they become gradually closer together towards the tapered extremity.

Ruedemann (1925, p. 76) suggested that the specimen might belong 'with the filamentous appendages of unknown connection with the eurypterids described by Clarke and Ruedemann (1912, p. 314) from the Shawangunk grit, and which offer a suggestion of similarity with the supposed combs of the Carboniferous *Glyptoscorpius* as described by Peach'. An examination of the figures of Clarke and Ruedemann (1912, pl. 53, figs. 10-17) and Peach (1883, pl. 29, figs. 17, 17*a-c*, 18, 20, 20*a*) shows only a superficial resemblance between these forms and NYSM 9627. The specimen does not appear to belong to any of the eurypterid species recorded from the Kokomo Waterlime (Kjellesvig-Waering 1948). It may represent an arthropod appendage but its nature and affinities remain unknown.

Anomalocaris? emmonsi (Walcott, 1886)

Plate 81, fig. 12

v. 1886 *Climacograptus?? Emmonsi* Walcott, pp. 15, 46, 51, 93, 94, pl. 11, fig. 5.

1938 *Anomalocaris? emmonsi*; Resser and Howell, p. 232.

Holotype. USNM 92727, Plate 81, fig. 12, original of Walcott 1886, pl. 11, fig. 5.

Other material. Unknown.

Locality and stratigraphical horizon. Lower Cambrian, Lower Parker Slate, *Olenellus* Zone, Noah Parker Quarry, 150 ft above the base of the Parker Slate Formation (Shaw 1955), on Parker Cobble, west-north-west of Georgia Center, Milton quadrangle, Vermont (see Shaw 1954, 1958 for an account of the formation).

DESCRIPTION

The poorly defined outline of the specimen (Pl. 81, fig. 12) is elongate, apparently tapering to a point in one direction and incomplete in the other. Twelve or thirteen 'divisions' are defined by corrugations which traverse a longitudinal axis at an angle of about 80°. The axis is gently curved and preserved in positive relief. It is displaced to one side suggesting that the outline of the specimen may be incomplete, if it were originally bilaterally symmetrical. The corrugations form projections in positive relief, and the intervening troughs indentations which may be partly the result of a covering of matrix. The oblique angle at which the divisions traverse the axis give the specimen a superficially spirally coiled appearance.

DISCUSSION

USNM 92727 was originally interpreted by Walcott (1886, p. 51) as a graptolite, and provisionally referred to the genus *Climacograptus*. Resser and Howell (1938, p. 232), however, stated that 'this small unique specimen . . . is too poorly preserved to be fully identified . . . Careful study indicates that it is a crustacean and probably *Anomalocaris*.' Ruedemann (1947, p. 53) accepted that the specimen had 'been recognized by Resser as not belonging to the graptolites', and R. B. Rickards (pers. comm.) agrees with this rejection. The relief and morphology, although poorly preserved, do not support Resser and Howell's (1938) contention that the specimen is either crustacean, or that it can be referred to *Anomalocaris*. It may represent an alga but, in the absence of better-preserved evidence of the outline and morphology, its nature and affinities remain problematical.

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